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The correlation of learning speed and natural foraging success in bumble-bees

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Despite the widespread assumption that the learning abilities of animals are adapted to the particular environments in which they operate, the quantitative effects of learning performance on fitness remain virtually unknown. Here, we evaluate the learning performance of bumble-bees (*Bombus terrestris*) from multiple colonies in an ecologically relevant associative learning task under laboratory conditions, before testing the foraging performance of the same colonies under the field conditions. We demonstrate that variation in learning speed among bumble-bee colonies is directly correlated with the foraging performance, a robust fitness measure, under natural conditions. Colonies vary in learning speed by a factor of nearly five, with the slowest learning colonies collecting 40% less nectar than the fastest learning colonies. Such a steep fitness function is suggestive of strong selection for higher learning speed. Partial correlation analysis reveals that other factors such as forager body size or colour preference appear to be negligible in our study. Although our study does not directly prove causality of learning on foraging success, our approach of correlating natural within-species variation in these two factors represents a major advance over traditional between-species correlative analyses where comparability can be compromised by the fact that species vary along multiple dimensions.

Keywords: adaptive value; associative learning; fitness measures; flower colour; learning speed; nectar foraging behaviour

1. INTRODUCTION

Learning, or the adaptive modification of behaviour based on experience, affects virtually every aspect of animal behaviour. However, despite the abundance of research on the mechanisms of learning in a wide variety of animal taxa, we still know very little about how learning performance is actually adapted to real ecological conditions (Shettleworth 1998; Dukas 2004). As different individuals or species vary widely in their learning capacities, it is commonly assumed that these differences reflect adaptations to the natural conditions under which such animals operate (Gallistel 1990; Dukas 1998; Shettleworth 1998). While it is intuitively appealing to assume that such variation in learning performance is adaptive (Johnston 1982; Dukas 1998), few studies have yet been conducted to specifically examine this link under natural conditions.

Laboratory studies, using grasshoppers (Dukas & Bernays 2000) and parasitoid wasps (Dukas & Duan 2000), suggest that animals able to form associations between cues (such as colour, odour or location) and rewards perform better than animals prevented from learning. Other laboratory studies, applying artificial selection to the learning ability of fruitflies, provide evidence for potential fitness costs associated with enhanced performance in associative learning (Mery & Kawecki 2003, 2004) or long-term memory (Mery & Kawecki 2005) tasks. While these results suggest that the ability to learn is useful (compared with being unable to learn) in highly controlled laboratory situations, and that enhanced learning appears to incur higher costs, they do not yet inform us directly about the potential fitness pay-offs for animals with different learning abilities under natural conditions. Circumstantial evidence for the adaptive value of learning comes from between-species comparisons (Dukas & Real 1991; Sherry & Healy 1998; Healy *et al.* 2005): for example, vole species with larger home ranges typically have better spatial memory, and their hippocampi (brain areas that store spatial memories) are typically larger (Sherry & Healy 1998). While such studies suggest that learning performance and ecologically important measures (such as home range size) are correlated, the species compared also vary in numerous other ecological requirements. Therefore, to make further progress in understanding the evolutionary and ecological relevance of learning abilities, we must quantify how and to what extent learning differences within species affect animal fitness in nature (Papaj & Prokopy 1989; Dukas & Duan 2000).

Here, we directly correlate variation in learning performance with field foraging performance (a robust measure of fitness) for multiple bumble-bee colonies (*Bombus terrestris*). In our laboratory learning trials, the bees' task was to overcome their innate preference for blue (Lunau *et al.* 1996; Chittka *et al.* 2004; Raine *et al.* 2006*a*) and learn to associate yellow as a predictor of floral reward. This is a simple associative task that bumble-bees are able to learn, but individuals and colonies vary in their speed and accuracy (Chittka *et al.* 2004; Raine *et al.* 2006*b*). The task is ecologically relevant because foraging bees use a variety of cues, including floral colour, pattern and scent, to recognize, discriminate and learn the flowers from which they collect

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food (nectar and pollen; Menzel 1985; Chittka & Raine 2006). As social insects, reproduction is restricted to a subset of individuals within each bumble-bee colony. Hence, intercolony (rather than inter-individual) variation in performance forms the raw material upon which any selection for learning ability could act.

2. MATERIAL AND METHODS

(a) *Learning performance*

We obtained 12 bumble-bee (*Bombus terrestris dalmatinus*) colonies, each containing 30–40 workers, from Koppert Biological Systems (Berkel en Rodenrijs, The Netherlands). Prior to experiments, bees were fed pollen and artificial nectar ad libitum without exposure to coloured stimuli associated with food. All workers were uniquely marked on the thorax with numbered, coloured tags (Opalith tags; Christian Graze KG, Germany). This allowed individuals to be accurately identified in both laboratory learning experiments and field foraging trials.

The bees were pre-trained to forage from 20 bicoloured, blue and yellow, artificial flowers in a laboratory flight arena. The square, bicoloured flowers were constructed from two halves (each 12×24 mm): one yellow (Perspex Yellow 260) and the other blue (Perspex Blue 727). During pre-training, all bicoloured flowers were rewarded with 50% (w/w) sucrose solution providing previously colour-naive bees with an equal chance to associate both colours with reward (Raine *et al.* 2006*b*). Bees completing at least five consecutive foraging bouts on bicoloured flowers were selected for training. These foragers were trained individually, in a flight arena containing 10 blue (Perspex Blue 727) and 10 yellow (Perspex Yellow 260) artificial flowers (each 24×24 mm). Yellow flowers were rewarding (each contained 15 µl of 50% (w/w) sucrose solution), while blue flowers were empty (unrewarding). Bees were regarded as choosing a flower when they either approached (inspected) or landed on it. Landing on a flower did not necessarily result in a feeding (probing) event. Therefore, before probing a rewarding (yellow) flower, bees could choose both yellow/rewarding or blue/unrewarding flowers by approaching or landing on them (without probing). Choosing a yellow (rewarding) flower was regarded as 'correct', while choosing a blue (unrewarding) flower was deemed to be an 'error'. We recorded the choice sequence made by each bee from the time it first entered the flight arena. Recording the flower choices for each bee ceased once it had made 99 flower choices after the first time it probed a rewarding (yellow) flower (Raine *et al.* 2006*b*). Therefore, each bee made at least 100 flower choices, including the first time it probed a rewarding flower, plus any choices made before this first probing event.

Flowers were changed and their positions re-randomized between foraging bouts to prevent bees using scent marks or previous flower positions as predictors of reward. Flower colours were selected so that bees had to overcome their strong, unlearned preference for blue, before associating one of their innately least favoured colours (yellow) with reward (Chittka *et al.* 2004; Raine *et al.* 2006*a*). Fifteen bees were trained from each colony (i.e. 180 bees in total) between 4 and 24 July 2005. Thorax width measurements were taken for each of these bees as a measure of body size. Controlled illumination for laboratory experiments was provided by high-frequency fluorescent lighting (TMS 24F lamps with 4.3 kHz ballasts (Philips, The Netherlands) fitted with Activa daylight tubes (Osram, Germany)) to simulate natural daylight above the bee flicker fusion frequency.

(b) *Learning curves*

The starting point for each bee's learning curve was the proportion of errors made (blue flowers chosen) before the bee first probed a rewarding (yellow) flower. For bees making fewer than five flower choices (either by approaching or landing on them) before probing a rewarding flower ($n=53$), we used the colony mean proportion of errors (calculated from bees making five or more such choices). Flower choices made by each bee after (and including) the first time it probed a rewarding (yellow) flower were evaluated as the number of errors (blue flowers chosen) in each group of 10 choices. Learning curves (first-order exponential decay functions: $y=y_0+Ae^{-x/t}$) were fitted to these 11 data points (i.e. the start pointing and subsequent 10 groups of 10 flower choices) for each individual bee, using MICROCAL ORIGIN (Chittka *et al.* 2004; Raine *et al.* 2006*b*), to capture the dynamic nature of the learning process. Here, x is the number of flower choices the bee made, starting with the first time it probed a yellow flower, and y is the number of errors. The saturation performance level (y_0) is the number of errors made by a bee after finishing the learning process, i.e. when reaching a performance plateau. The decay constant (t) is a measure of learning speed: high values of t correspond to slow learning, whereas lower t values indicate faster learners. A is the curve amplitude: the maximum displacement (height) of the curve above y_0. Both amplitude (A) and saturation performance (y_0) were constrained between 0 and 10 for curve fitting. Eight (out of 180) bees showed no appreciable improvement in performance during the task, and the software generated 'learning curves' that were essentially horizontal lines. These bees were excluded from subsequent analyses because their t values were either very high (>400) or negative.

To validate our curve fitting approach, we reanalysed learning data using an alternative methodology. In this approach, we assessed the number of flower choices taken by each bee (after the first time it probed a yellow flower) to reach an 80% improvement in task performance from its starting level. Starting performance levels for each bee were calculated as above, while the final performance level was taken as the number of errors during the last 10 recorded flower choices. A 10-choice moving average was calculated across the 100 flower choices (including the first time a rewarding flower was probed) for each bee (i.e. choices 1–10, 2–11, …, 91–100). The moving averages were compared sequentially against the 80% task improvement criterion. This provided the number of flower choices made by each bee before it reached its own 80% improvement criterion. We found a strong correlation between this 'curve-free' measure of learning speed and the t values generated from fitted learning curves (Pearson's correlation: $r=0.484$, $n=172$, $p<0.005$). Thus, the bees determined as fast learners by curve fitting (i.e. those with low t values) also took fewer flower choices to reach their 80% improvement criterion. We therefore use t values as a robust measure of learning speed throughout this study.

(c) *Field foraging performance*

The nectar foraging performance of the same 12 colonies for which we had obtained learning performance data was assessed by allowing them to forage in the environment around Queen Mary College (E1 4NS, London, UK). Once outside the nest, bees could forage freely in an area

containing large numbers of flower species in bloom growing in numerous private gardens, several large parks and other areas of open land (e.g. canal or railway embankments). Therefore, bees made the same foraging decisions they would face in more 'natural' habitats, namely where to forage and which flowers to visit in a diverse and abundant flower market whose resources are patchily distributed in space.

Foraging performance was measured for six colonies per day for 12 days between 25 July and 6 August 2005 (heavy rain prevented data collection on 27 July). Two sets of six colonies were assigned at the start of the experiment, and the performance of each set was assessed on alternating days (i.e. six colonies per day for 12 days = 72 colony days in total). On each day of data collection, all bees were allowed to leave test colonies from 09.00 to 17.00 hours, after which data were recorded only for incoming bees until all returned or 19.00 hours. Any bees returning later were reintroduced to their nest the following morning. For each colony, bee traffic was controlled by means of shutters in the entrance tube, so that all exiting and returning foragers could be captured and weighed. As far as possible, all bees that wished to forage were allowed to do so. Observers monitored the time and mass of each individual forager when it departed, and returned to, the nest from each foraging bout. As they departed and arrived, the bees were captured in plastic vials and transferred to an electronic balance (Ohaus Navigator N20330; Ohaus Corporation, Pine Brook, NJ; accuracy ± 2 mg) to measure their body mass. Departure time was taken when the bees were released after weighing and the time of arrival when the bees first reappeared at the nest. Although individual foragers can collect nectar, pollen or both, the bees in this study collected predominantly nectar only. This was an intended result of providing all colonies with ad libitum pollen, so that we could collect as large an amount of comparable nectar foraging data as possible. Observers measuring foraging rates were entirely blind to the learning performance of each colony as assessed in the first part of the experiment.

In bumble-bees, the amount of food brought into the colony has a very strong influence on the output of sexually active offspring (males and new queens: Schmid-Hempel & Schmid-Hempel 1998; Pelletier & McNeil 2003; Ings *et al.* 2006), thus tightly linking colony foraging performance and reproductive output. As such, foraging performance represents a robust proxy measure of fitness. We determined the foraging rate by dividing the difference in the forager's body mass (i.e. return minus outgoing mass) by the foraging trip duration (Ings *et al.* 2005, 2006). Nectar foraging rate was calculated on a per bout basis for each colony. This measure of performance is unaffected by the differences in overall colony size or the number of foragers leaving each colony. If the rate of colony nectar collection is the same, it does not matter if this rate is achieved by one forager performing 30 bouts or 30 foragers each completing a single bout. As such, we consider the foraging bout, rather than the individual forager, as the suitable unit of replication. To exclude orientation and defecation flights, we considered only trips lasting more than 5 min as foraging bouts (Capaldi & Dyer 1999; Spaethe & Weidenmüller 2002). Under this criterion, 40 (0.9%) trips were excluded, leaving 4394 foraging bouts (2843 hours of continuous foraging activity) for analysis.

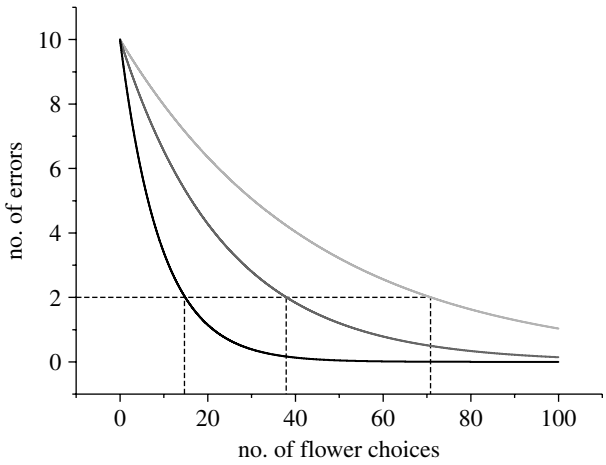

Figure 1. Learning speed of bumble-bee (*B. terrestris*) colonies. These curves illustrate how improvement in task performance over time relates to the learning speed, expressed as the decay constant (t) in the equation: $y = y_0 + Ae^{-x/t}$. The curves shown present the mean learning speeds for the fastest (D19: $t = 9.25$, black line), an intermediate speed (D17: $t = 24$, grey line) and the slowest (D11: $t = 44.07$, light grey line) learning colonies. All curves have amplitude (A) = 10, and saturation performance (y_0) = 0. Dashed lines indicate the average number of flower choices made by bees from each colony before achieving an 80% improvement in task performance.

3. RESULTS

We found significant variation among colonies in learning speed (t value: one-way ANOVA: $F_{11,160} = 1.900$, $p = 0.043$; see the electronic supplementary material). The differences in average learning speed between bees in these colonies were highlighted when we compared the number of flower choices taken to reduce the number of errors made by 80% from starting performance towards their saturation level (y_0, i.e. move 80% of the way from the top to the bottom of their learning curve). On average, bees from the fastest learning colony (D19) took only 15 flower visits to achieve an 80% improvement in task performance (from starting error levels), while bees from the slowest learning colony (D11) took 71 visits to reach the same performance criterion (figure 1). Therefore, these two colonies differed in learning speed by a factor of 4.7.

Nectar foraging rates of colonies allowed to forage under natural conditions varied significantly (one-way ANOVA: $F_{11,4382} = 17.87$, $p < 0.005$) with the most successful foraging colony bringing in almost three times more nectar than the least successful (means ± 1 s.e.m. = 257 ± 18 versus 87 ± 8 mg h^{-1}).

Most importantly, we found a significant correlation between learning and foraging performance, such that on average colonies with higher learning speeds (lower t values) brought in more nectar per unit time (Pearson's correlation: $r = -0.588$, $n = 12$, $p = 0.044$; line of best fit: nectar foraging rate $= -2.65t + 255.95$; figure 2). As foraging performance represents a robust proxy measure of fitness, this correlation suggests that higher learning speed is closely associated with increased bumble-bee colony fitness under natural conditions.

In other studies, worker body size has been shown to have a strong effect on foraging performance, with larger bees collecting proportionately more nectar

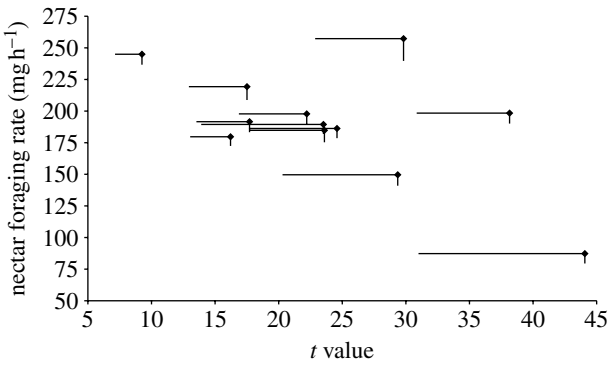

Figure 2. Correlation between learning speed and nectar foraging performance for 12 bumble-bee colonies. High t values correspond to slow learning, while low values are generated by fast learners. Data presented are colony mean values (-1 s.e.m.) for both t values and foraging performance. On average, colonies with higher learning speeds (lower t values) brought in more nectar per unit time (Pearson's correlation: $r=-0.588$, $n=12$, $p=0.044$).

(Spaethe & Weidenmüller 2002; Ings *et al.* 2005). Although the size of workers differed significantly among colonies in our study (thorax width from laboratory learning trials: one-way ANOVA: $F_{11,168}=8.407$, $p<0.005$; body mass of outgoing workers from field foraging trials: $F_{11,592}=18.276$, $p<0.005$), we found no correlation between mean forager size and either learning speed (thorax width: $r=-0.383$; $n=12$; $p=0.220$) or foraging performance (body mass: $r=-0.011$; $n=12$; $p=0.972$) among the 12 colonies. Furthermore, the partial correlation between colony learning and foraging performance remains significant when the potential effects of variation in worker body size are removed (partial correlation: $r=-0.641$, $n=12$, $p=0.034$). Thus, the colonies containing larger workers did not learn faster or collect more nectar in this study.

4. DISCUSSION

Our study assesses the potential adaptive value of the differences in learning performance under the real conditions in which animals operate. This represents a first step towards filling a fundamental knowledge gap regarding how cognitive ability is tuned to the environment. The positive correlation between colony learning speed and foraging performance suggests strong directional selection for higher learning speed in bumble-bees. Our results show that the slowest learning colonies brought in 40% less nectar than the fastest learning colonies.

However, as correlation does not necessarily indicate a causal relationship, we must consider alternative explanations for the observed pattern. Potentially, a spurious correlation could be produced between colony learning speed and foraging performance, if both these factors were correlated with a third variable. Body size could be one such variable, because previous studies indicate that larger bumble-bees are both more effective nectar foragers (Spaethe & Weidenmüller 2002; Ings *et al.* 2005) and have more sensitive eyes with greater visual acuity (Spaethe & Chittka 2003). However, although we found significant variation in worker body size (using both thorax width and body mass as indicators of body size) across the 12 colonies, we observed no significant correlation between body size and either learning speed or foraging performance in this study. The correlation between colony learning and foraging performance remained significant when the potential effects of intercolony variation in body size on both of these variables were removed by partial correlation. Parasitism represents another potential factor that could affect our correlation, as parasite infections appear to influence the foraging behaviour of bumble-bees (Schmid-Hempel & Schmid-Hempel 1990; Schmid-Hempel & Müller 1991; Schmid-Hempel & Stauffer 1998) and may also affect their ability to learn new associations (Mallon *et al.* 2003). The importance of 'parasite-free' colonies (Velthuis & van Doorn 2006) has lead to an effective 'zero-tolerance' policy to exclude parasites from *B. terrestris* commercial rearing facilities in Europe (K. Bolckmans 2007, personal communication, Koppert Biological Systems). Indeed, while parasites have been found in *Bombus impatiens* colonies produced by commercial breeders in North America (Colla *et al.* 2006), we know of no published records of gut parasites in commercial *B. terrestris* colonies and have found no evidence of parasites in any commercial *B. terrestris* colonies we have examined. Therefore, it is unlikely that our colonies were infected with parasites during the laboratory learning tests. This view is supported by our data, because the level of intercolony variation in learning speed among these 12 colonies is comparable to that shown by 16 colonies raised from wild-caught queens screened for gut parasites (Raine *et al.* 2006*b*). Once colonies were taken into the field to measure foraging performance, they were exposed to potential infection from parasites in the natural environment. However, while colonies might differ in their susceptibility to parasite infections in the same environment (Schmid-Hempel *et al.* 1999; Brown *et al.* 2000), exposure after completion of learning trials means that any differences in the levels of infection among colonies could only affect foraging (not learning) performance in our study. Recent results also suggest that variation among colonies in innate colour preference (for violet over blue) can affect foraging performance (Raine & Chittka 2007*a*). In our previous study, we tested the colour preferences and foraging performance of colonies raised from wild-caught queens in their natal habitat in which violet flowers produced considerably more nectar than blue flowers (Raine & Chittka 2007*a*). These results suggest that innate colour preferences of resident colonies are adapted to local floral rewards. However, in this study, we measured the foraging performance of commercially bred colonies, originally derived from a population native to the eastern Mediterranean, in a flora to which they had never previously been exposed. It therefore seems unlikely that these colonies would possess specific sensory traits to enhance foraging in this local environment.

Support for inferring a causative link between variation in learning speed and colony foraging success would be strengthened if we could demonstrate that colonies varied in some other behavioural trait (not involving learning) that did not correlate with either learning or foraging performance. In this study, we found significant variation among colonies in the number of workers recorded foraging from the bicoloured flowers during pre-training in the laboratory (one-way ANOVA: $F_{11,75}=9.615$, $p<0.005$), with the most active colonies sending out

more than four times as many foragers as the least active colonies (means $\pm$1 s.e.m. $=16.83\pm2.54$ versus 3.75 ± 0.77 foragers d^{-1}). Interestingly, there was no correlation between this variation in propensity to send out foragers (under laboratory conditions) with either colony learning speed (t value: Pearson's correlation: $r=-0.200$, $p=0.533$) or nectar foraging performance under natural conditions (Pearson's correlation: $r=0.225$, $p=0.483$). This finding suggests that overall levels of learning and/or foraging performance cannot simply be explained by variation among colonies in behavioural state, therefore providing further evidence to support the inference of causation between variation in learning speed and colony foraging performance.

As bees forage in a complex and dynamic pollination market in which floral rewards differ strongly among plant species and vary over time (Heinrich 1979; Willmer & Stone 2004; Raine *et al*. 2006*a*), individual foragers must assess such differences and respond accordingly (Chittka 1998; Menzel 2001; Chittka *et al*. 2003; Raine & Chittka 2007*b*). Rapid learning of salient floral cues, such as colour, presumably assists bees to track the changes in the floral rewards on offer, thereby improving bee foraging efficiency by allowing them to preferentially visit the current most profitable flower type (Raine *et al*. 2006*a*,*b*). It would be interesting to examine whether colonies that learn faster in visual tasks (e.g. learning colour associations) also show better learning performance in other modalities (e.g. odour or tactile cue learning). Laboratory studies (using the proboscis extension response paradigm) suggest that individual honeybees that are more sensitive to sucrose stimuli show improved learning in both odour and tactile conditioning experiments (Scheiner *et al*. 2001*a*,*b*). These results suggest that performance levels in an associative learning task using one modality might indeed be indicative of relative performance for other modalities, but this question deserves further direct investigation (ideally comparing learning performance using free flying bees).

To date, discussion of the potential adaptive value of learning has concentrated on the environmental conditions under which the learning (as opposed to no learning) will be favoured (Johnston 1982; Shettleworth 1998). However, these studies do not yet allow us to assess how the more subtle variation that exists between individuals in natural populations translates into fitness benefits. Some form of learning is predicted to be favoured in most environments, except those that are either too changeable that prior experience has no predictive value, or too consistent (across generations) that genetically preprogrammed innate behaviours alone are sufficient (Johnston 1982; Shettleworth 1998; Dukas 2004). Although simplistic, this (presence/absence of learning) framework appears sound because most animals demonstrate an ability to learn and operate in environments that change, but do not change so rapidly that the predictive value of forming associations becomes futile. The correlative approach used here is a first step to begin examining the fitness effects attributable to variation in learning performance under the real conditions to which animals are adapted. However, although our results suggest that variation in learning performance among bumble-bee colonies represents the most likely explanation for observed differences in their foraging performance, we need further evidence to establish a causal link. In future, it might be possible to selectively modify learning phenotypes, using double-stranded RNA interference (dsRNAi; Fire *et al*. 1998) or by creating more traditional knockout mutants (Raine *et al*. 2006*a*), and compare the foraging performance of wild-type and modified learning phenotypes. The choice of study organism for such an approach is a trade-off between availability of techniques and its tractability for fitness studies under natural conditions. While modifying the learning phenotype of fruitflies (*Drosophila* spp.) is more realistic in the short term, bumble-bees could be used to test effects of such modified learning phenotypes under more natural foraging conditions. Ultimately, in order to develop a more general understanding of the adaptive value of learning, we must directly examine the fitness effects of variation in learning performance across a range of animal species and the environments to which they and their learning performance are adapted.

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